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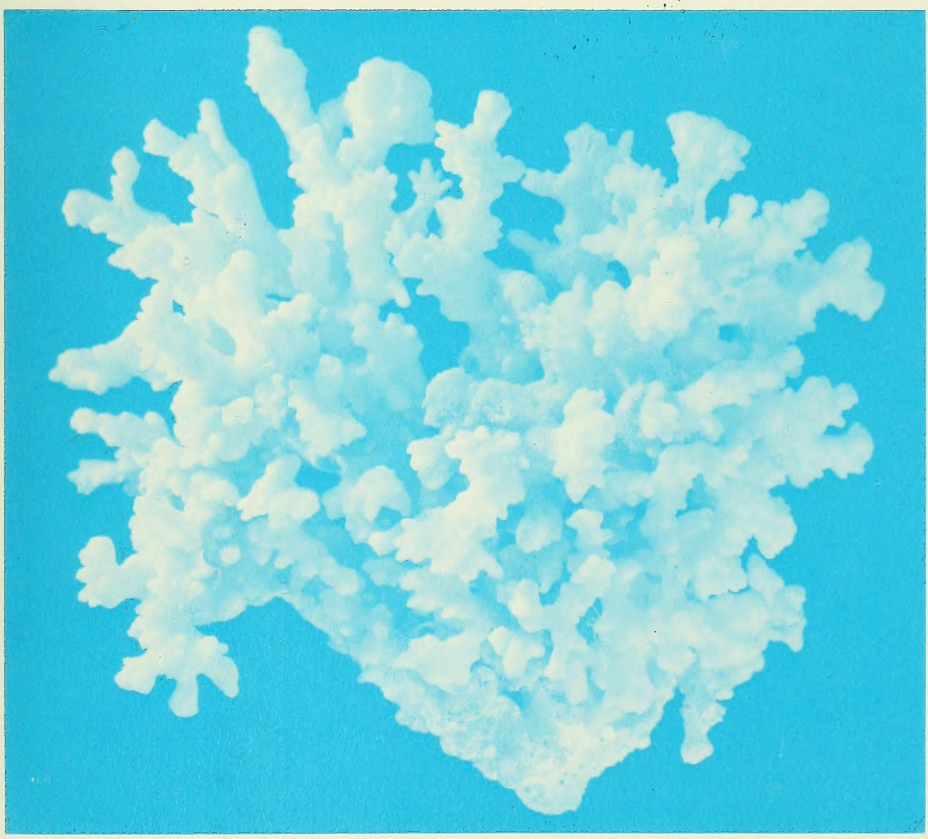

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New Upland Stream Frogs of the *Eleutherodactylus rugulosus* Group (Amphibia: Anura: Leptodactylidae) from Honduras

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Abstract.—A new species of the *Eleutherodactylus rugulosus* group is described from each of two montane sites in the Cordillera de Nombre de Dios and the Cordillera de Celaque of northcentral and southwestern Honduras, respectively. The northern form differs from the wide-ranging *E. rugulosus* in having vocal slits and nuptial pads in adult males (both absent in the latter) and in coloration. The Celaque species has a vocal slit but lacks nuptial pads in the only known adult male and is further distinguished from *E. rugulosus* and the other new form in hand morphology.

Savage (1975) reviewed the characteristics and distribution of the twelve species of Mexican and Central American stream frogs then thought to be allied to *Eleutherodactylus rugulosus.* The name *Eleutherodactylus berkenbuschii* subsequently was revived for *rugulosus*-like populations from Atlantic slope México that shared the following features: karyotype of 2 N = 22, a sharp canthus rostralis, the first finger usually shorter than the second and the dorsum smooth (Savage and DeWeese 1979). Two forms originally included in this complex (Savage 1975), *Eleutherodactylus matudai* and *Eleutherodactylus milesi,* were shown to form a distinct lineage not closely related to the *E. rugulosus* group and were placed in the *E. milesi* group (Miyamoto 1983; Savage 1987). An additional three species (*Eleutherodactylus anatipes, E. anomalus,* and *E. zygodactylus*) from the Pacific slope of northwestern South America recently were placed in the *E. rugulosus* group (Savage 1987). With these modifications, the *E. rugulosus* group now contains 14 species and ranges from tropical México, south through Central America to western Colombia and Ecuador.

Recent fieldwork in México, Guatemala, and the mountainous regions of Honduras has produced materials of several previously unknown species referrable to the *E. rugulosus* group. In the present paper we describe (definitions of character states follow Savage 1975, 1987) two of these new species from Honduras, the first of them to be called

Eleutherodactylus aurilegulus, sp. nov.

Holotype.—KU 209002, adult male, from Quebrada de Oro (15°38′N, 86°47′W), elevation 780–840 m, tributary of Río Viejo, south slope of Cerro Búfalo, Cordillera de Nombre de Dios, Departmento de Atlántida, Honduras, collected 14

August 1982 by James R. McCranie, Kenneth L. Williams, and Larry David Wilson. Original number LDW 6261.

Paratypes.—KU 209005, 209017–018, 209022, LACM 137293–294, adult males, and KU 209003–044, 209006–016, 209019–021, 209023, LACM 137286–292, 137295, adult females, from the type-locality, 780–1110 m.

Diagnosis.—A species having medium sized adult males (31–45 mm in standard length) and large adult females (60.7–80.5 mm) that is distinctive within the *E. rugulosus* group in having vocal slits and nuptial pads present in adult males, the first finger longer than the second, a rounded canthus rostralis, definite finger and toe disks, basal to moderate toe webbing, a pale yellow venter, and the posterior thigh surface usually blotched or mottled. The only other Mexican or upper Central American member of the group having vocal slits and nuptial pads in adult males is *Eleutherodactylus merendonensis* of northwestern Honduras. *E. aurilegulus* differs from the latter form (which has substantial toe webbing and fringed toes, strongly expanded finger and toe disks and a flap-like inner tarsal fold) in having basal to moderate toe webbing, ridges on the toe margins, much smaller finger and toe disks, and a strong but not flappable inner tarsal fold.

The new species resembles three lower Central American forms, *E. escoses, E. fleischmanni,* and *E. punctariolus* in the significant secondary features (presence of vocal slits and nuptial pads). *E. aurilegulus* is distinct from *E. escoces* (features for the latter in parentheses) most notably in coloration in having the venter pale yellow in life (bright red in adults) and the posterior thigh surface blotched, mottled, or spotted with light areas (uniform or suffused). *E. escoces* also has less toe webbing, with around 4½ phalanges free of the web on toe IV (ca. 4 in *aurilegulus*) and slightly smaller finger disks, no more than 1.5 times width of the phalanges (nearly twice width of phalanges in *aurilegulus*). From *E. fleischmanni* the new frog differs primarily in having larger finger and toe disks which are barely expanded in the former species. *E. punctariolus* has strongly expanded finger and toe disks and substantial webbing and fringes on the toes as compared to the smaller disks, basal to moderate toe webbing, and a ridge on toe margins in the new species.

E. aurilegulus is most likely to be confused with *E. rugulosus,* which generally occurs at elevations below 600 m along the Caribbean versant to the north of the Cordillera de Nombre de Dios in Honduras (Fig. 1) and has not been taken on the southern slopes of that range. The latter species is found however, from 500–2000 m in the central highlands of Honduras. *E. rugulosus* lacks vocal slits and nuptial pads in adult males and has the posterior thigh dark chocolate brown with discrete small to moderately large light spots. Adult male *E. aurilegulus* have vocal slits and nuptial pads and most examples of the species have a posterior thigh with a pattern of irregular light blotching and/or mottling. A few specimens have the thigh pale brown or tan with small light spots. In these examples the ground color is not as intense nor are the spots as clearly defined as in *E. rugulosus* from Honduras.

The Nombre de Dios endemic is distinguished from the second new form described in this paper in the diagnosis of the latter in a subsequent part of this account.

Summary of characteristics.—Dorsum granulate; canthus rostralis rounded; tympanum distinct; first finger longer than second; finger disks definite, almost

twice width of digit just proximal to disks on fingers III–IV; strong inner tarsal fold; toe disks definite, at least 1.5 times width of digit on toes III–V; toes with a marginal ridge; toes with definite basal to moderate webbing, modal webbing formula I 2–2½ II 2–3½ III 3–4+ IV 4+–2¾ V; paired vocal slits in adult males; nuptial pads in adult males; venter pale yellow, lightly punctated to heavily spotted with grayish or brown; throat lightly punctated to heavily pigmented with gray, grayish brown, or brown; dorsum pale olive brown to brown, uniform or spotted, some specimens with a thin yellow vertebral line; groin spotted or mottled; posterior surface of thigh usually blotched, or mottled sometimes with very small obscure light spots; underside of tibial segment clear, suffused, or barred; adult males 31–45 mm in standard length, females to 80.5 mm.

Coloration in life.—The coloration of the holotype (KU 209002) was as follows: dorsum pale olive brown with paler spot between shoulders and pale indication of interorbital bar; sides of body pale olive yellow, mottled with pale olive brown; venter pale yellow; throat white, mottled with pale brown and pale yellow; posterior surface of thighs brown, mottled with olive yellow; loreal region and lips pale olive yellow with brown bars; iris gold above, bronze below, separated by golden brown band. Two adult females (KU 209004, LACM 137286) were similar to the holotype except that LACM 137286 had a thin yellow vertebral stripe with the area around the stripe on the snout an ocher color. Another female (KU 209014) was colored as follows: dorsum dirty olive green with scattered rust red spotting; venter pale yellow with scattered gray punctations; throat pale grayish brown with white punctations; posterior surface of thighs brown with pale olive green mottling; upper lips with pale olive green and dark brown markings; soles of hands and feet gray; iris coppery bronze.

Measurements of holotype.—Standard length 44.8 mm; other measurements as percentages of standard length: head length 39.3; head width 38.4; orbit 13.2; snout length 17.9; loreal length 11.6; tympanum height 10.7; hindleg length 173.2; tibia length 58.0.

Measurements of paratypes.—Standard lengths are given in millimeters, other measurements as percentages of standard length (range followed by mean in parentheses). Standard length, 6 adult males 31.2–44.6 (40.7), 25 adult females 60.7–80.5 (68.8); head length, males 40.1–43.3 (41.0), females 38.6–46.9 (42.1); head width, males 36.7–39.1 (38.1), females 37.2–42.3 (39.9); hindleg length, males 171.4–183.4 (177.1), females 166.0–186.2 (175.4); tibia length, males 56.7–60.6 (58.4), females 54.2–61.6 (57.6).

Etymology.—The specific name *aurilegulus* is from the Latin meaning washing or bathing in gold because this species occurs along the margins of a golden stream, the Quebrada de Oro.

Natural history notes.—The vegetation at the type-locality is of the Subtropical Wet Forest formation of Holdridge (1967) and will be described in more detail by McCranie et al. (in prep.). Some members of the type series were collected during the day but were more frequently seen at night, especially during light rains. Specimens were collected in the water at the edges of the Quebrada de Oro, on the ground alongside the stream, and perched on large boulders in the stream. The known elevational range is 780–1110 m.

An adult female (KU 209003) was found on 4 June 1980 in association with a clutch of eggs in a dirt cavity in a crack of a huge flat rock. There are 80 eggs

in the clutch (KU 209034). The eggs were adherent to one another and lacked melanin deposits. Each egg capsule is about 6.5 mm in diameter, the ovum 4.4 mm.

Referred specimens.—Included here are juveniles and subadults from the Quebrada de Oro from between 780 and 1110 m as follows: KU 209024–027, LACM 137297, subadult males, KU 209028–29, 209031, LACM 137296, subadult females, and KU 209030, 209032–033, juveniles.

The second new form is to be known as

Eleutherodactylus anciano, sp. nov.

Holotype.—KU 208999, adult male, from El Chagüitón (14°30'N, 88°48'W), elevation 1830 m, 18.8 km SE Corquín, Cordillera, de Celaque, Departamento de Ocotepeque, Honduras, collected 25 May 1980 by James R. McCranie and Larry David Wilson. Original number LDW 5573.

Paratypes.—Royal Ontario Museum (ROM) 18076–079, adult females, from the type-locality, 1770–1830 m.

Diagnosis.—A species with medium sized adults (33 mm in standard length in a male, 32.8–41.2 in females) that differs from other members of the *E. rugulosus* group in having the following combination of character states: a single dextral vocal slit and no nuptial pads in the adult male; the first finger equal to or shorter than the second; definite finger and toe disks; moderate toe webbing; a pale yellow venter and the posterior thigh surface with discrete and contrasting small light spots on a dark brown field.

The only other Honduran species of *Eleutherodactylus* with which *E. anciano* might be confused is the wide-ranging (México to Panamá) and variable *E. rugulosus.* The new form differs from *E. rugulosus* (characteristics for this species in parentheses) in having a vocal slit in the adult male and finger 1 equal to or shorter than finger 2 (no vocal slits, finger 1 longer than 2). In addition *E. anciano* may be a smaller species than *E. rugulosus* since the latter includes adult males of 26–50 mm in standard length and females attain a size of 91 mm (in the samples of the new frog the only adult male is 33.0 mm in standard length and largest adult female is 41.2 mm, but the available series is small, $\bar{x} = 8$).

Eleutherodactylus anciano and *E. rugulosus* share the distinctive posterior thigh coloration of discrete, vivid light spots on a dark brown background. This pattern is also found in two other members of the *E. rugulosus* group, *E. berckenbuschii* of eastern México, and *E. brocchi* of Caribbean slope Guatemala. The new species resembles *E. berckenbuschii* in usually having finger 1 shorter than finger 2, but the latter lacks vocal slits in males, has a sharp canthus rostralis and the underside of the tibial segment of the leg is banded or boldly marked and suffused with dark pigment (vocal slit in adult male, rounded canthus rostralis, and the underside of the tibial segment barred, in *anciano*).

E. anciano is very different from the brightly colored *E. brocchi* (character states in parentheses) in having a vocal slit in the adult male, finger 1 shorter than finger 2, substantial toe webbing in adults (no vocal slits, finger 1 longer than finger 2, and practically no toe webbing) and in lacking large, light thigh spots, large dark spots on the throat and venter and the bright red coloration of the posterior venter and limb undersurfaces (large, bold light spots on thigh, throat, and venter with large dark spots, and bright red on posterior venter and lower surfaces of limbs).

The El Chagüitón species is not very similar to the other new form, *E. aurilegulus,* described in the present paper from northcentral Honduras and they may be readily distinguished on the basis of thigh pattern (distinct light spots on a dark field in *E. anciano* versus blotched, mottled or with very small, indistinct light areas in *E. aurilegulus*). In addition, *E. aurilegulus* has nuptial pads in adult males (absent in *E. anciano*) and has finger 1 longer than finger 2 (1 equal to or shorter than 2 in *E. anciano*).

Summary of characteristics.—Dorsum smooth to granulate; canthus rostralis rounded; tympanum distinct; first finger shorter than second or rarely equal in length; finger disks definite, almost twice width of digit just proximal to disks on fingers III–IV; strong inner tarsal fold; toe disks definite, at least 1.5 times width of digit on toes III–V; toes with a marginal ridge; toes with definite basal (juveniles) to moderate webbing, modal webbing formula I 2–2½ II 2–3+ III 3–4 IV 4–2½ V; a dextral vocal slit in adult male; no nuptial pads in adult male; venter white to pale yellow, immaculate; throat punctate to heavily pigmented with gray; dorsum olive green, tan, or rust brown, uniform, spotted, or mottled; groin spotted or mottled; posterior surface of thigh with small light spots on dark brown field; underside of tibial segment barred; adult male 33.0 mm in standard length, females to 41.2 mm.

Coloration in life.—The coloration of the four adult female paratypes was as follows: (ROM 18076) dorsum rust brown; venter cream; throat gray with white spots; posterior surface of thighs dark brown with cream spotting; upper surfaces of limbs rust brown with brown bands on legs; iris bronze with black reticulations: (ROM 18077) dorsum mottled dark and pale olive green with salmon pink spotting; venter pale yellow; throat white with gray punctations; posterior surface of thighs dark olive green with pale yellow spotting; iris dark bronze with dark reticulations; soles of hands and feet dark brown. Two other females (ROM 18078–079) were similar to ROM 18077 except that ROM 18078 had a pale olive green interocular bar. The coloration of three subadult males was as follows: (KU 209000) dorsum tan with pale brown mottling; pale brown interorbital bar; venter pearly white; posterior surface of thighs brown with yellow spotting: (KU 209001) dorsum grayish tan with brownish gray markings; sides of head with bronze patina; venter dirty yellow; throat pearly gray; iris bronze: (ROM 18080) dorsum olive green with rust red spotting; discontinuous rust red middorsal stripe; venter pale yellow; throat white with gray punctations; iris bronze with black reticulations; soles of hands and feet dark brown.

Measurements of holotype.—Standard length 33.0 mm; other measurements as percentages of standard length: head length 41.5; head width 40.6; orbit 14.8; snout length 17.9; loreal length 12.1; tympanum height 10.6; hindleg length 175.5; tibia length 59.1.

Measurements of paratypes.—Standard lengths for four adult females are given in millimeters, other measurements as percentages of standard length (range followed by mean in parentheses). Standard length 32.8–41.2 (37.9); head length 38.0–41.3 (40.0); head width 37.3–40.9 (39.3); hindleg length 180.5–197.1 (186.9); tibia length 59.4–62.6 (61.4).

Etymology.—The name *anciano* is an arbitrary combination of letters that happens to mean ancient in Spanish. The name is an allusion to Kenneth L. Williams, who has materially aided McCranie and Wilson in their efforts to

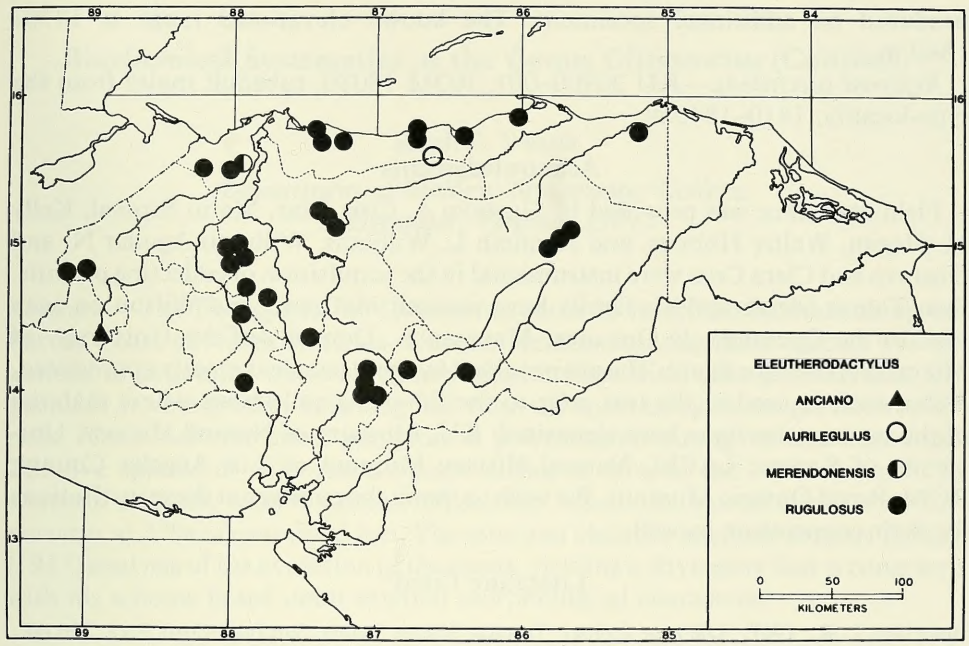

Fig. 1. Distribution of frogs of the *Eleutherodactylus rugulosus* group in Honduras.

elucidate the Honduran herpetofauna and helped in collecting the paratypes, and whose sobriquet is *El anciano.*

Remarks.—The condition of having a single dextral vocal slit as found in the male holotype of this species seems to be an anomaly. Additional material probably will prove that paired vocal slits are typical for the population since this is the condition in other members of the stock when the character is present.

The species is known from a single ridge (1770–1840 m) in the Cordillera de Celaque of southwestern Honduras (Fig. 1), very near to its boundary with El Salvador. Although *E. rugulosus* occurs at upland sites between 600–1370 m to the north in the Sierra Espíritu Santo and from 750–2000 m to the east of this site (Fig. 1), that species has not been collected in the vicinity of the Cordillera de Celaque or the adjacent Cordillera de Opalaca, even at lower elevations. Our decision to describe *E. anciano* involves a prediction that a distinctive allopatric montane population of the *E. rugulosus* group resembling the type series in significant features inhabits the Cordillera de Celaque and possibly the Cordillera de Opalaca as well.

Natural history notes.—All specimens of this species were collected alongside a small stream between two severely deforested hillsides presently used for pasturage. The original vegetation at the type-locality was of the Lower Montane Moist Forest formation of Holdridge (1967). Remnants of this vegetation occur on isolated hilltops in the area. The male holotype and one female paratype were collected during the day, the remaining specimens were found at night along the banks of or on rocks in the stream. The species is uncommon at the type-locality inasmuch as 6 nights of collecting in 3 different years produced only 6 specimens. Other streams in the area that were searched both in the daytime and at night

produced no additional specimens. The known elevational range is 1770–1840 m.

Referred specimens.—KU 20900–001, ROM 18080, subadult males from the type-locality, 1810–1840 m.

Acknowledgments

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Biochemical Systematics of the Genus *Clinocottus* (Cottidae)

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Abstract.—The five species of *Clinocottus* occur in intertidal habitats along the Pacific Coast of North America. Genetic variation among these species was examined to determine the evolutionary relationships within the genus. Allelic frequencies at nine protein-encoding loci were surveyed using starch gel electrophoresis. These loci were either polytypic or polymorphic among the taxa examined. The five species of *Clinocottus* shared alleles at 46% of the loci examined. In contrast, a closely related species, *Oligocottus maculosis,* shared alleles with *Clinocottus* at 27% of examined loci. Phenetic and cladistic analyses support Bolin's (1947) analysis of the evolution of the genus, yielding a phylogeny that is congruent with his scheme based upon external morphological characters.

The cottid genus *Clinocottus* includes some of the most common intertidal fishes of the Pacific coast of North America. It is comprised of five species with overlapping latitudinal distributions (Fig. 1). Four inhabit rocky intertidal areas, and one species (*Clinocottus acuticeps*), is found in sandy intertidal habitats (Miller and Lea 1972).

When originally described, the species were placed in various genera of the family Cottidae. However, Bolin (1947) recognized the unique common ancestry of these species (then in the genus *Clinocottus, Oxycottus,* or *Blennicottus*) and placed them together in the genus *Clinocottus.* He examined external morphological characters and identified three trends supporting his assessment of the evolutionary relationships within the genus: first, the progressive loss of such features as preopercular spines, scales, and the last gill slit; second, changes in the shape of the head from the primitive pointed profile to a hemispherical shape; and third, the enlargement and elaboration of the penis. Bolin's work involved subjective evaluation of complex characters displaying continuous intraspecific variation. The genetic basis of these characters is not known.

The present study reexamined the genus *Clinocottus* using an independent set of biochemical characters. Electrophoretic techniques have been shown to reveal protein characters that are particularly useful in biosystematic analyses because they occur as discrete alternative character states that have clear genetic basis (Nei 1987; Buth 1984). This study compares the five species of *Clinocottus* with *Oligocottus maculosus.* Evidence from larval and adult morphology indicates that *Oligocottus* and *Clinocottus* are closely related, cottid genera (Washington et al. 1984; Bolin 1947). This approach facilitates an objective assessment of the cohesiveness of the genus and the evolutionary relationships among its members.

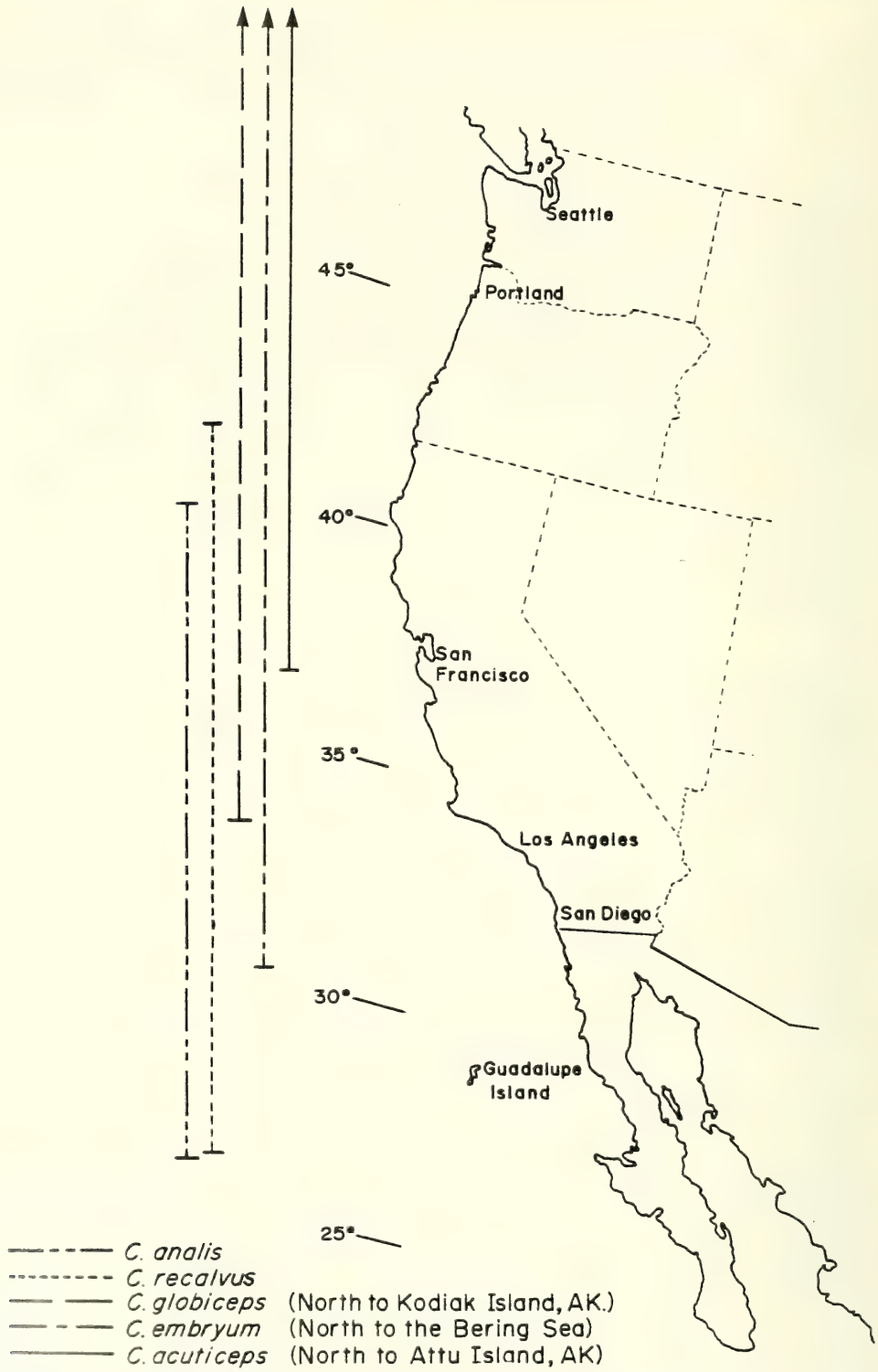

Fig. 1. Geographic distribution of species of the genus *Clinocottus* on the North American Pacific coast (from Miller and Lea 1972).

Methods and Materials

Specimens.—Fishes were collected in British Columbia and California from intertidal sites (listed below) in 1976 through 1978. In rocky intertidal habitats, fish were anesthetized with Quinaldine (2-Methylquinoline) and collected from tidepools with dip nets; *Clinocottus acuticeps* was collected from sandy habitats by beach seine. Specimens were either frozen immediately or transported alive to the laboratory for sacrifice. In some cases, individually tagged voucher specimens were deposited in the collection of the Natural History Museum of Los Angeles County. Tagged specimens received sequential numbers preceded by a letter indicating the collecting site (e.g., Pacific Grove specimens were indicated by the letter M). The numbers of specimens examined electrophoretically are enclosed in brackets. Sample sizes are larger for *Clinocottus analis* due to a concurrent study of intraspecific variation in that species (Swank 1979).

Clinocottus analis.—Pacific Grove, Ca., 36°39′N (LACM M) [N = 42]; San Simeon, Ca., 35°39′N (LACM SS) [N = 36]; Government Point, Ca., 34°26′N (LACM GP) [N = 30]; Palos Verdes, Ca., 33°42′N (LACM PV) [N = 50]; Santa Catalina Island, Ca., 33°27′N (LACM C) [N = 32]; East San Benitos Island, Baja California, 28°19′N (LACM Baja) [N = 21].

Clinocottus recalvus.—San Simeon, Ca., (LACM SS) [N = 3]; Government Point, Ca., (LACM GP) [N = 16].

Clinocottus globiceps.—Botanical Beach, British Columbia, 48°30′N (LACM BC) [N = 15]; Point Arena, Ca., 38°55′N (LACM PA) [N = 4]; Bodega Bay, Ca., 38°18′N (LACM B) [N = 2].

Clinocottus acuticeps.—Patricia Bay, British Columbia, 48°39′N (LACM BC) [N = 5]; Bazar Bay, British Columbia, 48°38′N (LACM BC) [N = 3].

Clinocottus embryum.—Botanical Beach, British Columbia (LACM BC) [N = 6].

Oligocottus maculosus.—Bodega Bay, Ca. (LACM B) [N = 5]; Sea Ranch, Ca., 38°40′N (LACM SR) [N = 34].

Electrophoretic procedures.—Each liver was removed, weighed, and homogenized in twice its volume of distilled water. All processing was carried out under refrigeration or on ice. Liver homogenates were centrifuged for one hour at 105,000 g in a Beckman Analytical Ultracentrifuge. The soluble protein fraction was removed and either subjected to electrophoresis immediately or frozen at −84°C until use. After removal of livers, the fish were individually tagged and frozen at −20°C. Just prior to electrophoresis fresh or frozen whole eyes were removed from each specimen and macerated.

Enzymes from liver and eye tissue were examined using horizontal starch gel electrophoresis. The procedures and enzyme stains were modified from Selander et al. (1971). A protein dye solution (1.0% hemoglobin, 1.0% albumin, and 0.5% bromphenol blue in 0.2 M Tris-HC1, pH 8.0) was placed in sample slots on each gel. The bromphenol blue marked the progress of the buffer front during electrophoresis, and the two proteins served as internal standards for the conditions of the run. Five enzymes coded by nine presumptive gene loci were examined, including four glucose-metabolizing enzymes: cytoplasmic malate dehydrogenase (one locus appeared: S-Mdh-A), cytoplasmic lactate dehydrogenase (three loci: Ldh-C, Ldh-B, Ldh-A), phosphoglucomutase (three loci: Pgm-1, Pgm-2, Pgm-3), phosphogluconate dehydrogenase (Pgdh-A); and one amino acid-metabolizing

enzyme, cytoplasmic asparatate aminotransferase (S-Aat-A). Locus nomenclature is based on recommendations for use in teleost studies (Buth 1983). Enzyme loci of unknown vertebrate homology were numbered in order of decreasing anodic mobility according to the convention of the International Union of Biochemistry (1984). The loci examined in the present study were those that yielded clear, unambiguous staining patterns in a preliminary survey using *Clinocottus analis.*

Gels to be stained for the enzymes MDH, AAT, PGM, and PGDH from the liver were run in phosphate buffer pH 6.7. Gels to be stained for any of the five enzymes from eye tissue were run in continuous Tris citrate buffered to pH 8.0. These buffer systems were described by Selander et al. (1971). Each allele identified was designated by its locus and its mobility relative to bromphenol blue (e.g., *Ldh-C (64)*). In order to determine whether two species shared alleles at a given locus, samples from species pairs were compared on the same gel. Eye macerates and liver extracts usually retained activity through successive freezings and thawings, thus permitting alternative comparisons and further verification of phenotypes. (Exceptions are noted in Results.)

Proteins having identical electrophoretic mobilities were treated as identical in the analysis. Allele frequencies were determined by direct count. Nei and Roychoudhury's (1974) minimum genetic distance measure (D_m) was used to assess the magnitude of genetic differentiation between species pairs. This measure is conservative, and the statistical significance of resulting distance values is testable by a chi-square test. In this analysis loci having a single allelic frequency greater than .95 were treated as monomorphic.

Cladistic analysis was accomplished by treating enzyme electromorphs (presumptive alleles) as characters with two states, present (1) and absent (0), in a species. Presence was defined as a minimum frequency of .05. These binary-coded characters were analyzed by Phylogenetic Analysis Using Parsimony (PAUP algorithm version 2.4.0, written by David L. Swofford, Illinois Natural History Survey). The branch and bound algorithm was used to find all most parsimonious trees from which a strict consensus tree was produced. Trees were rooted using *Oligocottus maculosus* as the outgroup.

Results

Nine presumptive loci encoding for five enzymatic proteins were assayed. These loci were either polytypic or polymorphic among the taxa examined. Allelic frequencies are presented in Table 1.

A unique allele of the S-Mdh-A locus was fixed in each of the five species of *Clinocottus* and in *O. maculosus.* The range of relative mobilities at this locus was small within the genus *Clinocottus* compared to the range of relative mobilities when *Oligocottus maculosus* is included (see Table 1).

LDH systems were scored exclusively from the eye macerates because no LDH activity could be consistently detected in liver extracts. LDH is a tetrameric enzyme composed of two types of polypeptide chains that are the products of two major structural gene loci (Ldh-B and Ldh-A). A third structural LDH locus (Ldh-C) is characteristic of the eye in many teleosts. These three LDH loci appeared in all the species examined except *C. acuticeps,* which showed no activity for Ldh-C. Because Ldh-C was present in *Oligocottus maculosus,* the absence of this locus in *C. acuticeps* was unexpected. This finding remains subject to further verification due to difficulties in obtaining *C. acuticeps.*

Table 1. Allelic frequencies at nine loci among five species of *Clinocottus* and *Oligocottus maculosus*.

Locus	Allele	*C. analis*	*C. recalvus*	*C. globiceps*	*C. embryum*	*C. acuticeps*	*O. maculosus*
Ldh-C	64	.997	—	—	—	—	1.0
	60	.003	.875	1.0	—	—	—
	59	—	.125	—	1.0	—	—
Ldh-B	44	—	—	—	—	1.0	—
	39	—	—	—	—	—	—
	36	.022	—	—	—	—	—
	31	.978	1.0	1.0	1.0	—	1.0
Ldh-A	27	—	1.0	1.0	1.0	1.0	1.0
	24	.997	—	—	—	—	—
	21	.003	—	—	—	—	—
Pgm-1	50	.447	—	—	—	—	—
	48	.447	—	—	—	—	—
	44	.105	—	—	—	—	—
	39	—	—	—	—	—	1.0
	33	—	—	1.0	—	—	—
	27	—	1.0	—	—	—	—
Pgm-2	31	—	—	—	.333	—	—
	30	—	—	—	—	—	.015
	28	.997	—	—	.667	—	—
	26	—	—	.225	—	—	—
	25	.003	—	—	—	—	.103
	23	—	—	.775	—	—	—
	21	—	1.0	—	—	—	—
	20	—	—	—	—	—	.882
Pgm-3	17	—	—	.083	—	—	—
	15	—	—	—	—	1.0	—
	13	.030	1.0	.917	1.0	—	—
	11	.960	—	—	—	—	—
	6	.010	—	—	—	—	—
S-Aat-A	52	—	.028	—	—	—	1.0
	51	—	.972	.950	1.0	—	—
	45	.994	—	.050	—	—	—
	41	.006	—	—	—	—	—
Pgdh-A	32	—	—	—	—	—	1.0
	31	.998	—	—	—	—	—
	28	.003	—	1.0	1.0	.667	—
	26	—	1.0	—	—	.333	—
S-Mdh-A	20.0	—	—	—	—	—	1.0
	16.0	1.0	—	—	—	—	—
	15.6	—	—	—	—	1.0	—
	15.2	—	—	—	1.0	—	—
	15.0	—	—	1.0	—	—	—
	14.0	—	1.0	—	—	—	—

As in mammals (Dawson and Mitchell 1969), *C. analis, C. recalvus,* and *C. globiceps* have three independent structural PGM loci. Staining revealed two PGM loci in *C. embryum* and *O. maculosus,* but only one PGM locus was detectable in *C. acuticeps.* In contrast to mammals which typically have three PGM loci, fishes having one or two PGM loci are widely reported in the literature (Lush

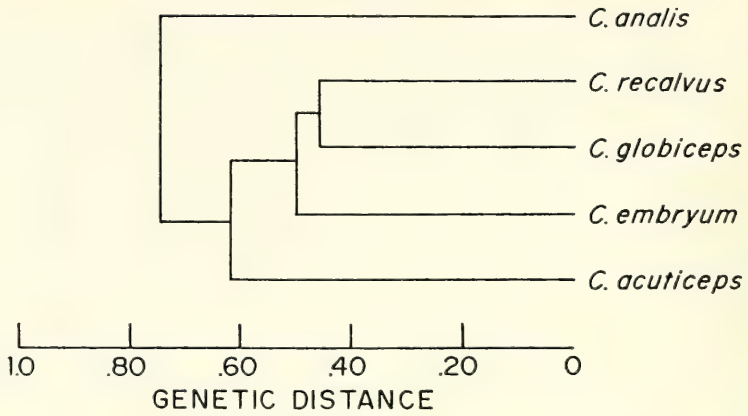

Fig. 2. Phenogram showing relationships among species of *Clinocottus* as derived from Nei (1974) minimum genetic distance values (D_m).

1969; Utter and Hodgins 1970; Avise and Selander 1972; Johnson 1975). Among species of *Clinocottus* having three loci with PGM activity, Pgm-1 and Pgm-2 had lower activity then Pgm-3. In samples that were frozen and thawed several times during the present study, no activity remained for Pgm-1 and Pgm-2. It is therefore possible that these loci are not consistently detected in fishes due to protein instability. The presence of three structural PGM loci in fishes may thus be more widespread than reported in other studies.

Although several regions of AAT activity appeared in some samples, staining was most intense for S-Aat-A. Two additional zones of activity appeared (having lower anodic mobility), but they could not be scored consistently and were disregarded in this analysis. The heterozygous phenotype for S-Aat-A was clearly three-banded, indicating its dimeric structure. Four S-Aat-A alleles were resolved. No S-Aat-A activity was present in *C. acuticeps.*

Three Pgdh-A alleles were resolved in the five species of *Clinocottus.* With the exception of *Pgdh-A* (*31*), which was unique to *C. analis,* these alleles were shared between species. A unique fourth allele *Pgdh-A* (*32*) was fixed in *Oligocottus maculosus.* Dimeric enzyme structure coded by a single locus was indicated by a three-banded phenotype in heterozygous individuals.

Clinocottus recalvus and *C. globiceps* shared more alleles than any other species pair. These two species shared an allele at each of five loci (56% of the loci examined). Four of these alleles were also shared with *Clinocottus embryum* (see Table 1). *Clinocottus analis* and *C. acuticeps* each shared one of these alleles with the *globiceps-recalvis-embryum* group (not including one very rare allele, *Pgm*3 (13), in *C. analis*). With the exception of another very rare allele *Pgdh-A* (28)), *C. analis* shared none of the resolved alleles with *C. acuticeps.* Phenetic relationships among the five species of *Clinocottus* based upon genetic distance (D_m) are illustrated in Fig. 2. These values are based on the available data for all loci examined in the present study.

Due to larger sample sizes in *Clinocottus analis,* eight rare alleles appearing at frequencies less than .05, were detected at seven of the nine loci examined. Three of these rare alleles (*Pgdh-A* (*28*), *Pgm-3* (*13*), *Ldh-C* (*60*)) were fixed in one or more of the other species in the genus. One allele (*Pgm-2* (*25*)) was shared only

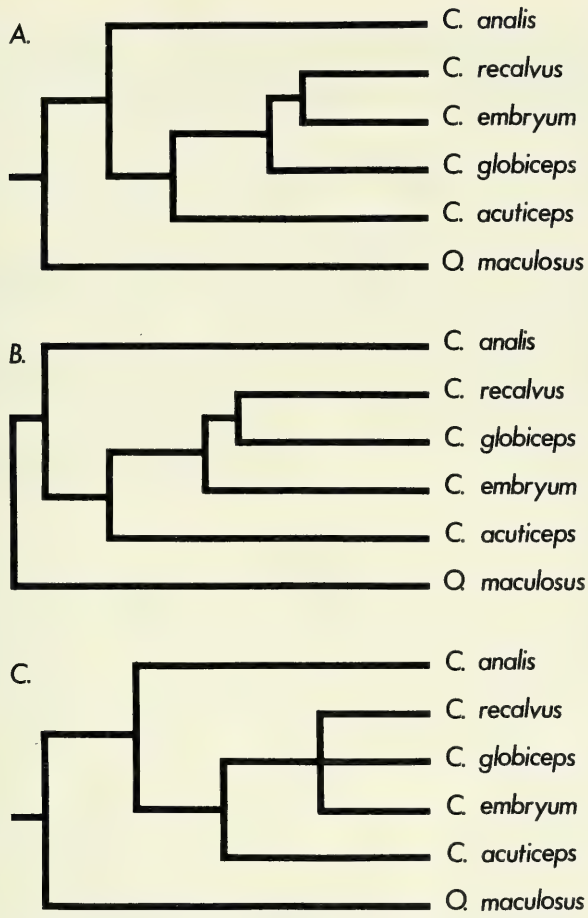

Fig. 3. Two equally parsimonious trees (A and B) and strict consensus tree (C) expressing cladistic relationships among species of the cottid genus *Clinocottus* based on binary coding of 37 electromorph products. The trees are rooted with *Oligocottus maculosus* as the outgroup. The consistency index for A and B is .865 and the length is 37.

as an uncommon allele in *Oligocottus maculosus.* The remaining alleles (*Ldh-B* (*36*), *Ldh-A* (*21*), *Pgm-3* (*6*), *S-Aat-A* (*41*)) were unique to *C. analis.*

Cladistic analysis yielded two equally parsimonious trees and a strict consensus tree represented in Fig. 3. Phenetic and cladistic analyses yield the same relative pattern of species relationships.

Discussion

Shared alleles have been widely used in the phylogenetic analysis of electrophoretic data (see Buth 1984). Avise and Smith (1974) reported that nine closely related species of the sunfish genus *Lepomis* shared alleles at about 50% of their loci. Comparably, the five species of *Clinocottus* share alleles at an average of 46% of the loci examined. In contrast, *Oligocottus maculosus* shares alleles with *Clinocottus* at only 27% of the loci examined, corresponding to the greater evolutionary distance between the two genera than within the genus *Clinocottus.* Since

Oligocottus maculosus shares known alleles with *Clinocottus* only at the three LDH loci, this value may underestimate the true evolutionary divergence. LDH may be evolutionarily conservative in these species since the levels of LDH polymorphism are low.

Both phenetic and cladistic analyses (Figs. 2 and 3, respectively) strongly support Bolin's (1947) views on the evolution of the genus *Clinocottus.* These analyses of protein characters yield a phylogeny that is congruent with Bolin's (1947) analysis based upon external morphological characters. The species of the *recalvus-globiceps-embryum* group were placed in the subgenus *Blenicottus* by Bolin (1944). These species are separated by genetic distances of .501 or less. *Clinocottus acuticeps,* the sole number of the subgenus *Oxycottus* (Bolin 1944), is joined to the *Blenicottus* group at .620 genetic distance units. Genetic distance measurements support Bolin's conclusion that *C. analis* (subgenus *Clinocottus*) is the most divergent number of the genus, joining the *Blenicottus* group at genetic distance of .753. The two most divergent members of the genus, *C. analis* and *C. acuticeps,* are separated from one another by a genetic distance of .968.

The relatively small number of loci surveyed in the present study limits the inference derived from these phenetic results. Gorman and Renzi (1979) found that genetic distance values were more subject to sampling error when few loci were surveyed. More information could be obtained in future studies of the genus *Clinocottus* by sampling additional gene loci.

Cladistic analysis using alleles as characters further supports Bolin's subgeneric designations (see Fig. 3). Cladistic analysis was also performed using loci as characters. However, this method was too conservative, and the consensus tree yielded no useful information.

Bolin (1944) regarded the genus *Clinocottus* as boreal in origin. Genetic divergence within the genus may be associated with the invasion of new habitats. The three species of *Clinocottus* with the greatest genetic similarity share the presumed ancestral habitat (rocky intertidal areas of boreal and temperate latitudes). *Clinocottus recalvus* and *C. globiceps* are separated by less genetic distance than other members of the genus. *C. embryum* is closest to *C. globiceps* with which it shares the greatest overlap in geographic range (see Fig. 1). Although *C. recalvus* ranges farther south, these three species cooccur between Gaviota, California and Brookings, Oregon (Miller and Lea 1972). Two more divergent members of the genus may have invaded new habitats: *C. analis* is common in warmer latitudes, and *C. acuticeps* lives in ecologically distinct sandy habitats.

In the present study, *Clinocottus analis* shared only one common allele (*Ldh-B* (*31*)) with other species of *Clinocottus.* However, the larger sample size *C. analis* permitted the detection of three rare alleles shared with other members of the genus (*Ldh-C* (*60*), *Pgm-3* (*13*) and *Pgdh-A* (*28*)). The genetic distance measure (Nei and Roychoudhury 1974) utilizes allelic frequency data; rare alleles have very little effect on genetic distance. Nevertheless, the identification of rare alleles shared with congeneric species may be important in elucidating the mechanisms of evolutionary divergence between species. Lewontin (1974) suggested that many of the genetic differences between closely related species are derived from polymorphisms in ancestral species. Biochemical divergence among the members of the genus *Clinocottus* appears to have followed this pattern. The distribution of alleles at Pgdh-A and Ldh-C loci suggest that species differences may have evolved

from ancestral polymorphisms (see Table 1). For example, one of the two Pgdh-A alleles found in *C. acuticeps* was present in each of the other species of *Clinocottus*. At the Ldh-C locus each species carries either *Ldh-C (60)* or *Ldh-C (59)* or both alleles. Such allele distributions are most readily explained by hypothesizing a polymorphic ancestral species carrying both alleles, either of which may have been lost in derivative species.

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Rediscovery of the Shoshone Pupfish, *Cyprinodon nevadensis shoshone* (Cyprinodontidae), at Shoshone Springs, Inyo County, California

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Abstract.—The Shoshone pupfish, *Cyprinodon nevadensis shoshone,* has been considered extinct since prior to 1970. The subspecies, however, apparently survived precariously for an extended period in a nearly impenetrable marshy outflow below Shoshone Springs and increased following reestablishment of favorable habitat conditions. Pupfish, found in large numbers throughout the Shoshone Springs system in summer 1986, most closely resembled *C. n. shoshone.* In passing through a genetic "bottleneck" the modal number of caudal fin-rays shifted from 18 to 16. All other meristic characteristics are essentially unchanged from the original description.

Most of the pupfishes (genus *Cyprinodon*) of the Death Valley drainage system (Miller 1948, 1981) have been under stress since World War II, as burgeoning human populations invaded western deserts and, directly or indirectly, affected delicate aquatic ecosystems and their biotas (Cook and Williams 1982; Deacon and Deacon 1979; Miller and Pister 1971; Pister 1974, 1981; Soltz and Naiman 1978). Except on the floor of Death Valley, where four distinctive pupfishes occur (Miller 1948; LaBounty and Deacon 1972), populations of *Cyprinodon* have undergone drastic reductions through habitat modification or destruction or by competition with and predation by exotic organisms (mosquitofish, largemouth bass, sailfin mollies, crayfish, and bullfrogs) (Baugh et al. 1986; Williams and Deacon 1986; Williams and Sada 1985a, b). Two subspecies of the Amargosa pupfish, *Cyprinodon nevadensis* Eigenmann and Eigenmann, have been reported extinct: the Tecopa pupfish, *C. n. calidae* Miller, and the Shoshone pupfish, *C. n. shoshone* Miller (Pister 1974). The former was the first organism to be declared officially extinct under provisions of the U.S. Endangered Species Act of 1973 (Federal Register 1982, 47:2317–2319). The latter was never formally listed by the U.S. as extinct because it was considered gone before the Endangered Species Act was passed.

The objective of this paper is to review the history of the depletion of the Shoshone pupfish and to examine the question of its extinction by analyzing recently caught samples of pupfish from the outlet of Shoshone Springs.

The Shoshone pupfish, *Cyprinodon nevadensis shoshone* (Miller 1948), occurred throughout the outflow of Shoshone Springs and was considered common by

Miller in 1938. Miller (1967), however, could find no specimens in the area in January 1966 or July 1967 though he reported that Robert Ornduff of U.C. Berkeley found pupfish to be fairly common in the lower reaches of the [outlet] stream near its junction with the Amargosa River sometime during 1966. Miller (1970) considered the subspecies as probably extinct by November 1969. Selby (1977), during extensive collections in the area in 1977, failed to find any pupfish though introduced mosquitofish were abundant as noted earlier (1966–67) by Ornduff and Miller. Based upon its presumed extinction, the U.S. Fish and Wildlife Service never added this pupfish to its List of Endangered and Threatened Wildlife. Our recent collections (July 1986) in the area have found pupfish to be common to abundant in the spring outflow from below the Old State Highway downstream to, and throughout a "permanent" water segment of the Amargosa River near Shoshone found by Miller (1948) to be dry in 1939 (Fig. 1).

Three alternative hypotheses can be used to explain the occurrence of pupfish in these waters:

1. pupfish from another area reached Shoshone via a surface water connection during or following a flood;
2. pupfish from another area were introduced into Shoshone waters by man;
3. pupfish maintained a small population in Shoshone waters but remained undetected until recently.

The geographic proximity of Tecopa and the Amargosa Canyon makes it most probable that if hypotheses 1 or 2 were correct, the pupfish at Shoshone would most closely resemble *C. n. amargosae.* If hypothesis 3 is correct, the pupfish at Shoshone would most closely resemble *C. n. shoshone.*

Description of the Study Area

Shoshone Springs and their outlet creek (Fig. 1) are near the base of a volcanic hill on the northern outskirts of the town of Shoshone, Inyo County, California. The spring source, at an elevation of about 518 m, has been enclosed for more than 48 years by a series of concrete boxes that direct most of the flow to supply the town of Shoshone and the local swimming pool. The small stream issuing from the spring source passes under the Old State Highway and, enhanced by outflow from the swimming pool, proceeds for about 400–500 m to the bed of the Amargosa River. Here elevation is less than 487 m and, on 31 July 1986 channel width varied from about 8 cm to 1.5 m, depth 8 cm to 0.5 m. Conductivity was about 2959 umohs/cm with a pH of 8.2. Chlorine concentration at the Old State Highway was detectable, but less than 0.4 ppm. Water temperature on 31 July 1986 was 34°C at an air temperature of 39°C. In mid winter the temperatures may fall to 28°C in this section (Miller 1948).

Between the Old State Highway and State Highway 127, the channel is confined to a concrete ditch. Below Highway 127, the stream enters a dense cattail marsh and then a nearly impenetrable tamarisk thicket before joining the stream bed of the Amargosa River. During summer 1986 water occurred in the river bed for a distance of approximately 1.5 km N to 3–4 km S of Shoshone. Pupfish occurred from a point below the Old State Highway downstream throughout the area described above.

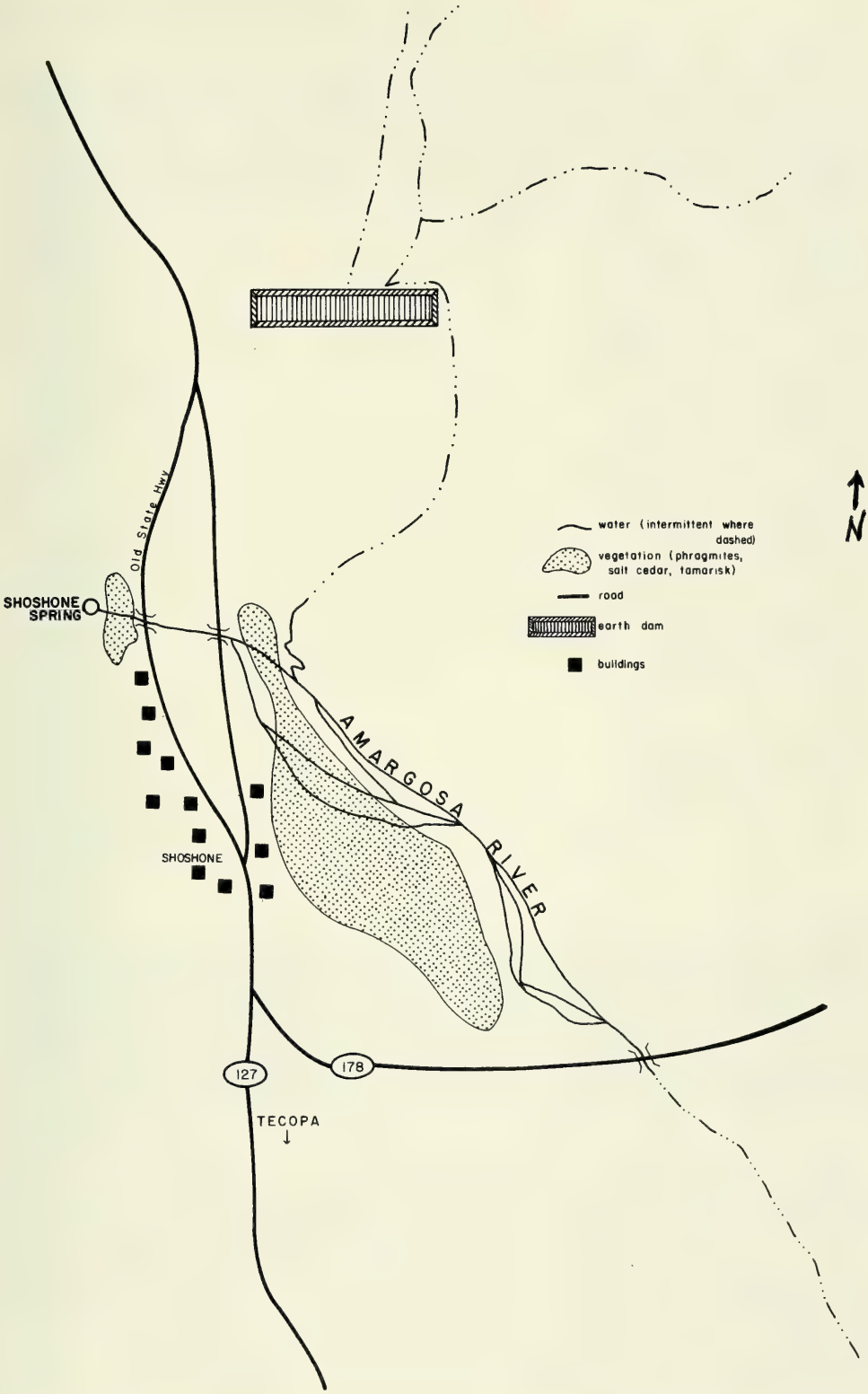

Fig. 1. Sketch map of Shoshone Springs, the outlet creek and the bed of Amargosa River.

Table 1. Comparison of fin ray counts from two populations of *Cyprinodon nevadensis* collected about 50 years apart. Early data are from Miller (1948). S = outflow of Shoshone Springs, T = Tecopa Bore, A = Amargosa River near Tecopa. (Miller combined data from the 1939 and 1942 collections for Amargosa River near Tecopa.)

Character	Location	Date	0	1	2	3	4	5	6	7	8	9	10
Dorsal fin rays	S	7/31/86										7	40
		1/29/39										28	94
	T	7/31/86										0	1
	A	5/16/39 and 5/30/42										3	64
Anal fin rays	S	7/31/86				1					2	5	34
		1/29/39				0					0	10	104
	T	7/31/86				0					0	0	7
	A	5/10/39 and 5/30/42				0					0	1	62
Caudal fin rays	S	7/31/86											
		1/29/39											
	T	7/31/86											
	A	5/16/39 and 5/30/42											
Pectoral fin ray	S	7/31/86											
		1/29/39											
	T	7/31/86											
	A	5/16/39 and 5/30/42											
Pelvic fin rays	S	7/31/86	6	0	2	13	13	20	58	5	3	0	
		1/29/39	37	1	0	3	4	32	169	12	0	0	
	T	7/31/86	0	0	0	0	0	9	53	39	16	3	
	A	5/16/39 and 5/30/42	0	1	0	1	6	29	151	11	1	0	

Methods

Fish were collected with seines, traps, and dipnets on 31 July 1986. Meristic characters were utilized to compare the pupfish at Shoshone with *C. n. amargosae* collected from Tecopa Bore, and with data presented by Miller (1948). Sixty specimens of each population were analyzed employing the methods of Miller (1948) for the following characters: dorsal, anal, caudal, pectoral, and pelvic finrays; numbers of scales around the body and around the caudal peduncle.

Table 2. Comparison of circumference of body scale counts from two populations of *Cyprinodon nevadensis* collected about 50 years apart. Early data from Miller (1948).

		Circumference of body scales					
Locality	Date	18	19	20	21	22	23
Shoshone Springs outflow	31 July 1986	2	2	7	7	7	12
	9 Jan. 1939	0	1	2	4	21	21
Tecopa Bore	31 July 1986	0	2	0	3	7	9
Amargosa River near Tecopa	16 May 1939 and 30 May 1942	0	0	0	0	0	2

Table 1. Extended.

11	12	13	14	15	16	17	18	19	20	21	22	23	No.	M S.E.
13	0	0											60	10.01 ± .07
12	0	0											134	9.88 ± .05
29	28	2											60	11.52 ± .08
31	2	0											100	10.32 ± .06
18	0												60	10.02 ± .14
19	0												133	10.07 ± .04
39	14												60	11.12 ± .07
37	0												100	10.36 ± .05
			1	9	29	17	8	1	0	0	0	0	60	16.42 ± .13
			0	0	14	32	53	14	6	1	0	0	120	17.74 ± .09
			0	0	1	10	21	21	6	0	0	1	60	18.43 ± .14
			0	0	9	18	44	19	9	1	0	0	100	18.04 ± .11
			3	8	33	11	4	0					59	16.09 ± .12
			0	42	134	36	2	0					214	15.99 ± .04
			0	4	13	32	10	1					60	16.85 ± .10
			1	23	120	49	4	0					197	16.16 ± .05
													120	5.03 ± .15
													258	4.98 ± .13
													120	6.59 ± .08
													200	5.82 ± .04

Results

Miller's description of *C. n. shoshone* as a subspecies "with a slab-sided and rather slender body, and with the arch of the ventral contour much less pronounced than that of the dorsal contour," coupled with seemingly distinctive behavioral characteristics in aquaria, first alerted us to the possibility that pupfish from Shoshone were distinct from those collected at Tecopa Bore.

We, therefore, returned to the Shoshone, Tecopa area to make collections for taxonomic analysis. Meristic data (Tables 1, 2) indicate that fish collected at

Table 2. Extended.

Circumference of body scales								
24	25	26	27	28	29	30	No.	M ± S.E.
7	11	4	0	0	0	0	60	22.78 ± .29
20	7	6	2	0	0	0	84	23.25 ± .17
7	15	7	3	1	0	1	60	24.02 ± .26
12	17	24	26	12	5	2	100	26.26 ± .15

Shoshone in 1986 are closest to *C. n. shoshone* as described by Miller (1948). In addition, our sample from Tecopa Bore is closest to Miller's (1948) description of *C. n. amargosae*. Where differences exist with Miller's (1948) description, the two populations retain relative, but not absolute differences.

The Shoshone population differs from the Tecopa Bore population in having lower mean numbers (±2 SE) of pelvic, dorsal, and caudal fin-rays.

Discussion

The pupfish population in the outflow of Shoshone Springs most closely resembles *C. n. shoshone* as described by Miller (1948). We therefore suggest that the population probably has maintained itself continuously in those waters. The failure of Miller (1967), Selby (1977), and others to locate the fish may have been a consequence of small population sizes when the area was examined. There is evidence of considerable habitat disruption in the past. Installation of a concrete channel below Old State Highway, presence of detectable chlorine from the outflow of the Shoshone swimming pool, concrete boxes at the spring source, heavy equipment operating in the area during fall 1986, and a deeply eroded Amargosa River channel all demonstrate that considerable natural and man caused habitat disruption has been common in the outflow of Shoshone Spring over the past 40 years. The subspecies has demonstrated considerable resiliency. We suggest that with careful planning and sensitivity to maintaining the remaining habitat, the Shoshone pupfish could continue its existence as one of the oldest, most characteristic inhabitants of Shoshone, California.

The most striking difference between the 1986 Shoshone sample and all previous collections from this spring system lies in the number of caudal fin-rays: strongly modal at 18 in all previous samples (1891–1969) but 16 in the 1986 collection. Examination of caudal-ray counts for all subspecies of *Cyprinodon nevadensis* (Miller, 1948: Table XVIII), involving 1929 specimens, revealed a modal count of 16 only for the Bradford's Spring race of the Ash Meadows pupfish, *C. n. mionectes* Miller. However, this low number was in part due to the small size of specimens available for examination. The caudal fin is the last of the fins to attain complete branching of the rays. This explanation is supported by counts of the caudal fin-rays of 29 adults from Bradford's Spring (UMMZ 158430, collected 21 May 1977): 16 (1), 17 (5), 18 (15), 19 (7), 20 (1). These details are given to eliminate the highly unlikely possibility that the present pupfish stock in Shoshone Springs originated by introduction from Bradford's Spring.

We hypothesize that the change in number of caudal fin-rays resulted from reduction of the original population of Shoshone pupfish to a very low level. Passage of this population through such a genetic bottleneck may have resulted in release of dominance and epistasis variance with subsequent selection pressures favoring 16-rayed, rather than 18-rayed individuals. It is probable that other isolated populations of Death Valley pupfishes have experienced similar bottlenecks, resulting in rapid morphological change, in recent years. Williams (1977) demonstrated morphological changes in a refugium population of Devils Hole pupfish originating from 25 transplanted adults. That such changes may not be uncommon is suggested by the recent report by Lewin (1987) of increased morphological variance in houseflies following a severe bottleneck.

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A Cluster Analysis of Pacific Ocean Temperatures and North American Upper Air Temperatures

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Abstract.—Twenty-two years of summer North Pacific Ocean temperatures were cluster analyzed with fall North American 700 mb air temperatures. Several regional groups were identified on the linkage tree. Most of these groups were aligned in east-west latitudinal bands. One cluster linked both water and air temperatures, suggesting possible teleconnections between ocean and atmosphere.

Many articles have been published recently on the topic of ocean-air interaction. The Southern Oscillation/El Nino events have been given much attention in the literature (e.g., Yarnal and Diaz 1986; Namias and Cayan 1984; Van Loon and Madden 1981; Chiu and Lo 1979). Other studies have centered on the use of sea surface temperature (SST) anomolies as a predictive tool in long range weather forecasting (Namias and Cayan 1981; Walsh and Richman 1981; Davis 1976). Davis (1978) has suggested that seasonally stratified data be employed to detect any predictive associations that may exist between the ocean and atmosphere. A variety of statistical techniques have been utilized to investigate these interactions (Nicholls 1987; Diaz 1981; Weare et al. 1976; Hannes 1974; Namias 1973).

The major objectives of this paper are twofold: first, to examine the relationships, if any, that exist between the ocean and atmosphere, and second, to describe the various regional groups that are formed by cluster analysis. Cluster analysis has not been used extensively in ocean-air interaction studies. According to Wolter (1987), cluster analysis has not been used extensively because of the inability to test the statistical significance of the cluster procedure.

Methods

This study uses summer mean water temperatures located in the North Pacific Ocean east of the International Date Line (180°). Samples were taken along the 50th, 40th, 30th, and 20th parallels. Summer in this report refers to the average water temperatures for the months of June, July, and August. Twenty-two years of seasonally averaged sea surface temperatures for fifteen locations were calculated from data obtained from *Fishering Information* (1962 to 1980) and *Oceanographic Monthly Summary* (1980 to 1983).

Fall upper air temperatures for twenty-two locations were calculated from monthly data obtained from *Monthly Climatic Data for the World* (1962–1983). The fall average represents the months of September, October, and November. Fig. 1 depicts the locations of the sampling sites.

The seasonally averaged data were normalized and then cluster analyzed. The computer program used was originally written by Mather (1976). This program

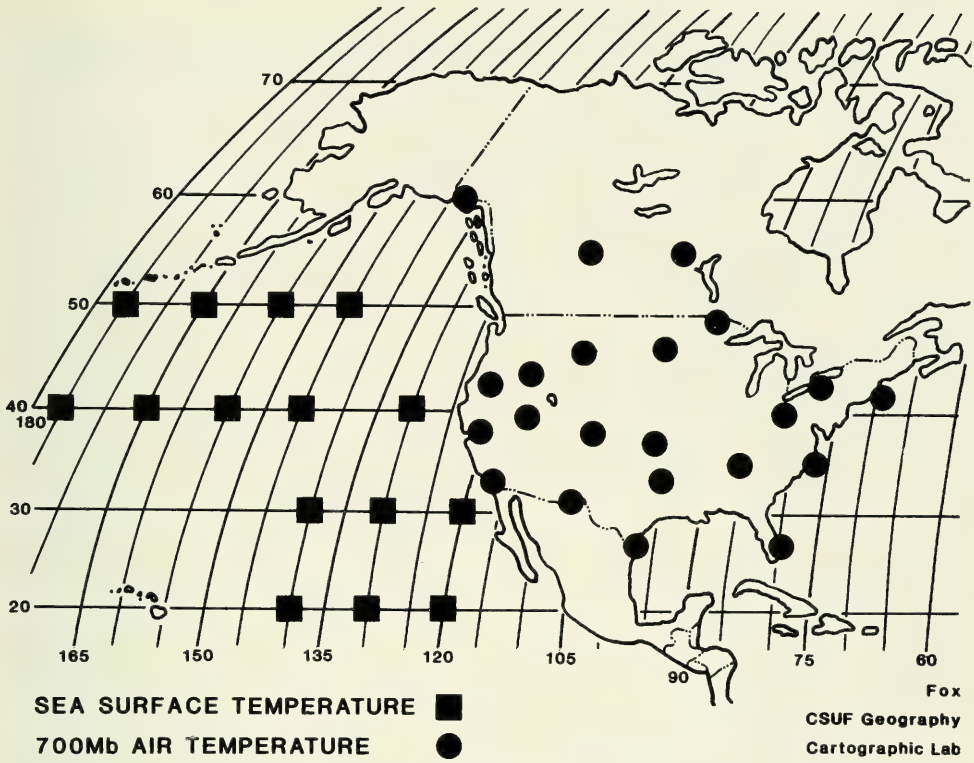

Fig. 1. Study area.

is listed and described in his book. The major purpose of cluster analysis is to select subsets of mutually similar data from a larger set of all such data. A cluster or group is initially formed by the most similar pair; other clusters are formed based on similarity coefficient. Thus, over time all the data will form one large group at a higher similarity coefficient. Therefore, by using cluster analysis, significant groupings can be formed (Hannes and Hannes 1984).

Results and Discussion

The results of cluster analysis are presented in the form of a linkage tree (Fig. 2). The upper air locations and SST locations form the vertical axis; the similarity coefficients are along the horizontal. Locations that are most similar pair off at low similarity coefficients. Each cluster is joined with another at larger and larger coefficient values until one large cluster is formed at a value of 10.4 (Fig. 2). Using a similarity coefficient value of approximately 0.113, six groups are formed (Fig. 2). Group one is made up of Bismark, Great Falls, Buffalo, Boise, Medford, and Nantucket. Group two consists of Grand Junction, Ely, Nashville, North Platte, Oklahoma City, Cape Hatteras, and Oakland. Group three consists of El Paso, San Diego, Miami, Brownsville, and SST sampled along the 50th parallel. The fourth group begins with SST located at 40°N, 155°W and ends with 30°N, 130°W. The fifth cluster contains water temperatures found at 20°N, 130°W; 20°N, 140°W; 30°N, 140°W, and 20°N, 120°W. Edmonton, International Falls, The Pas, and Yakutat, all upper air stations, make up the last group.

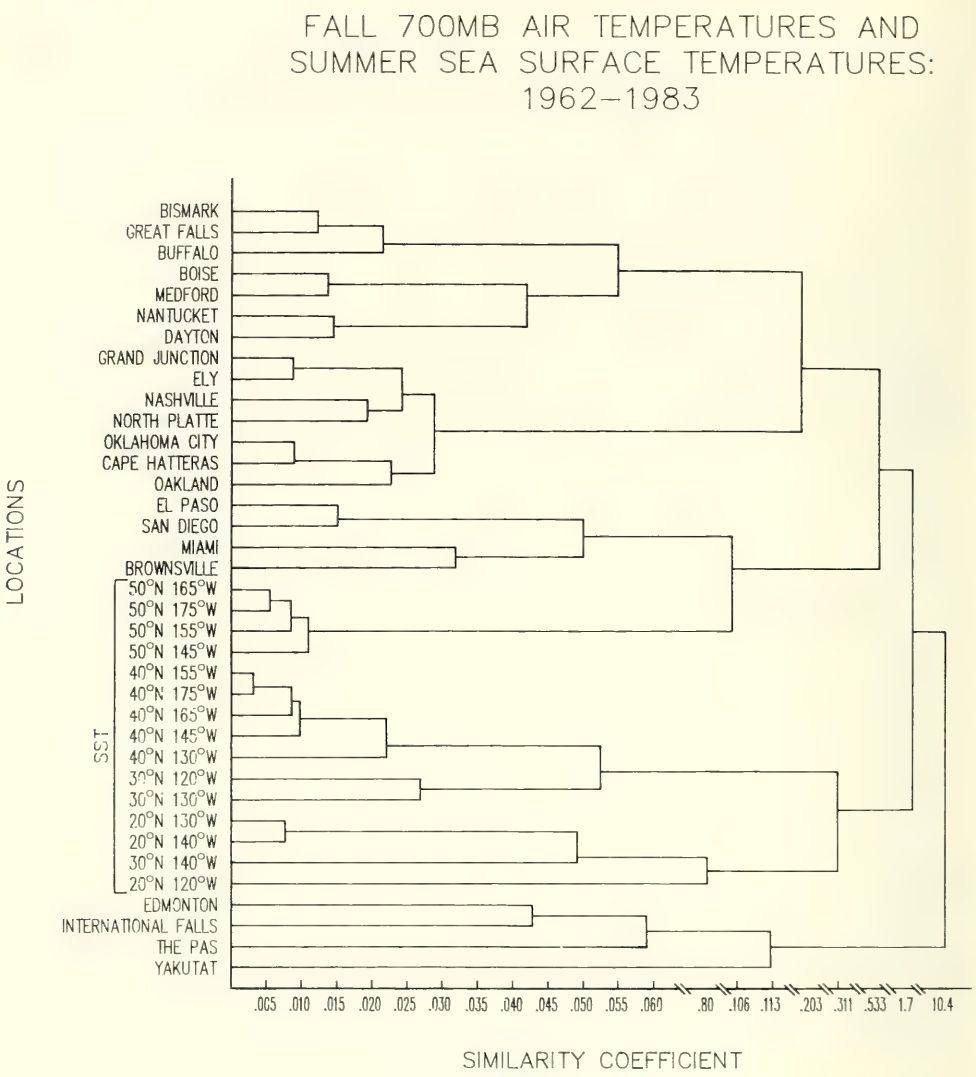

Fig. 2. Linkage tree.

Two basic questions come to mind concerning the various groups. First, what do the clusters represent? Secondly, what physical factors are responsible for these clusters? All the groups, except group three, represent latitudinally organized bands. This suggests the influence of earth-sun geometry and the distribution of insolation as a major cause of the east-west alignment. This alignment is typified by group two (Grand Junction, Ely, Nashville, North Platte, Oklahoma City, Cape Hatteras, and Oakland; Fig. 2).

Clusters four and five also latitudinally organized, appear to represent the mean position of the Japanese and California Ocean Currents (Espenshade 1982). Group five consists mostly of SST's located at 20°N latitude. This position generally marks the transition between the California and North Equatorial Currents (Espenshade 1982).

The only cluster that contains both upper air and SST's is cluster number three. Low latitude upper air temperatures sampled at El Paso, San Diego, Miami, and Brownsville are linked with high latitude (50°N) water temperatures. This cluster possibly represents some form of teleconnection between ocean and atmosphere. Teleconnections that exist between various northern hemisphere atmospheric variable and SST's have been described by several authors. For instance, Fritz (1982) has shown that northern hemispheric winter 700 mb heights are related to Pacific Ocean temperatures. Likewise, Diaz and Namias (1983) have examined the seasonal relationships between surface air temperatures and western northern hemispheric 700 mb heights. They found that during the summer a positive relationship existed between eastern United States surface air temperatures and heights in the western northern hemisphere polar regions. Furthermore, Walsh and Richman (1981) found associations between northern Pacific SST anomolies and surface temperature fluctuations over the southeastern and far western portions of the United States. Thus, the linkage of SST and upper air temperatures shown in Fig. 2 probably represents a similar form of teleconnection as suggested by the previously mentioned authors.

This study has shown that cluster analysis is a useful technique for identifying regional or coherent patterns of climate and oceanic variables as well as a tool for examining possible teleconnections between the ocean and atmosphere. Spatial coherence of climatological data can be easily identified on a linkage tree as typified by group two (Fig. 2). Therefore, cluster analysis can be employed in a similar fashion as either factor analysis or empirical orthogonal analysis (Weare et al. 1976; Walsh et al. 1982). Future studies that employ cluster analysis will likely focus on three broad areas of applications: 1) the determination of the number of groups, 2) the statistical significance of these groups, and 3) the evaluation of the different types of clustering procedures.

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Erratum

From the Organisms of a Subtidal Sand Community in Southern California, we have an incorrect address for Jon E. Kastendiek.

It should read: Marine Review Committee, Inc.
531 Encinitas Blvd.
Encinitas, California 92024

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The Hermatypic Coral *Pocillopora* at Cabo San Lucas, Mexico

The hermatypic scleractinian coral *Pocillopora* Lamarck, 1816 has a recorded geographic range as living in the eastern Pacific Ocean from the Gulf of California at Bahía Los Frailes (Fig. 1) on the east coast of Baja California Sur, Mexico, north to Isla San Marcos in the Gulf, and south along the mainland and offshore islands of Mexico, Central America, and South America to Ecuador (Durham and Barnard 1952; Squires 1959). At Bahía Pulmo (Fig. 1), the bay adjacent to Bahía Los Frailes, it is the most abundant coral in the celebrated coral reefs first described by Steinbeck and Ricketts (1941), who apparently learned of them from the "Coast Pilot" (U.S. Hydrographic Office 1928), or one of its supplements, which noted that "a coral reef projects in a northeasterly direction, and ends about 1/2 mile eastward of Cape Pulmo . . ." Subsequently, several specialists (Durham 1947; Durham and Barnard 1952; Squires 1959; Brusca and Thompson 1977) have refined the northern geographic range of the genus *Pocillopora* in the eastern Pacific and mentioned or studied various aspects of the Bahía Pulmo reefs.

Squires (1959), who extended the range of *Pocillopora* from Bahía Pulmo to Bahía Los Frailes, a distance of approximately two kilometers, also indicated (op. cit. table 3) the presence of this genus and two other tropical genera, *Cycloseris* and *Pavona,* on the west coast of the Baja California peninsula. That these indications are erroneous is shown by the absence of any confirming localities under his (Squires 1959) very detailed geographic distribution records for each species of the three genera. No other report exists of these genera on the west coast of the peninsula. Among the hermatypic corals of the Gulf of California, only *Porites* is known from the west coast of the Baja California peninsula, where it occurs, living and fossil, at Bahía Magdalena (Jordan 1936; Squires 1959). However, on Isla Guadalupe, an oceanic island 275 km off the west central coast of the Baja California peninsula, *Pocillopora* is an abundant Pleistocene fossil (Squires 1959; Durham 1980), although no longer living there. Isla Guadalupe, at 29°N, is therefore the northernmost record for the genus in the eastern Pacific.

The geographic range of *Pocillopora* on the Baja California peninsula is here extended 80 km SSW of Bahía Los Frailes in the Gulf of California to Cabo San Lucas (Fig. 1) at the margin of the Pacific coast of the peninsula. The coralla (Fig. 2) there occur on a granite substrate, much of which is vertical. They grow to large sizes (1–2 m in diameter) and are common but isolated in distribution, perhaps because of somewhat cooler water temperatures at Cabo San Lucas than on the coast to the northeast. Robinson (1973) indicated a low mean sea surface temperature at Cabo San Lucas of 68°F (20°C) in February. The influences at Cabo San Lucas of a major submarine canyon and longshore currents moving south on the Pacific side of the cape may produce cooler local temperatures.

Pocillopora also is abundant and previously unreported on the intervening coast between Cabo San Lucas and Bahía Los Frailes, growing in reef-like luxuriance at Punta Palmillas, Bahía Chileno, and Bahía Santa Maria (Fig. 1).

At Punta Palmillas, large, 1–3 m diameter, crowded, intergrown coralla of *Pocillopora* (Fig. 3) form incipient fringing reefs developed on systems of short,

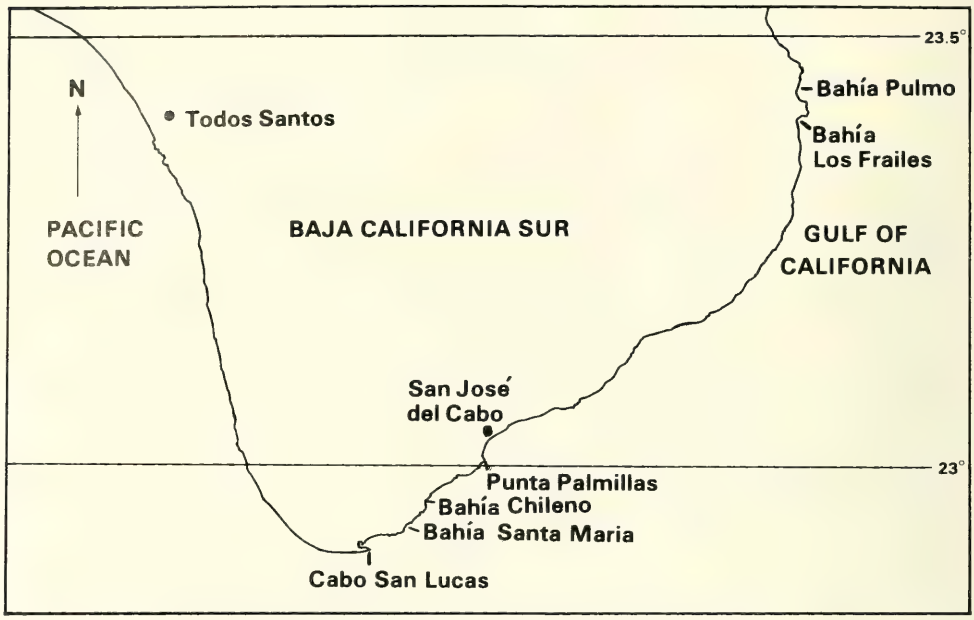

Fig. 1. Map of southern coast of Baja California Sur, Mexico showing locations of places mentioned in text. Distance between latitude lines shown is approximately 50 km.

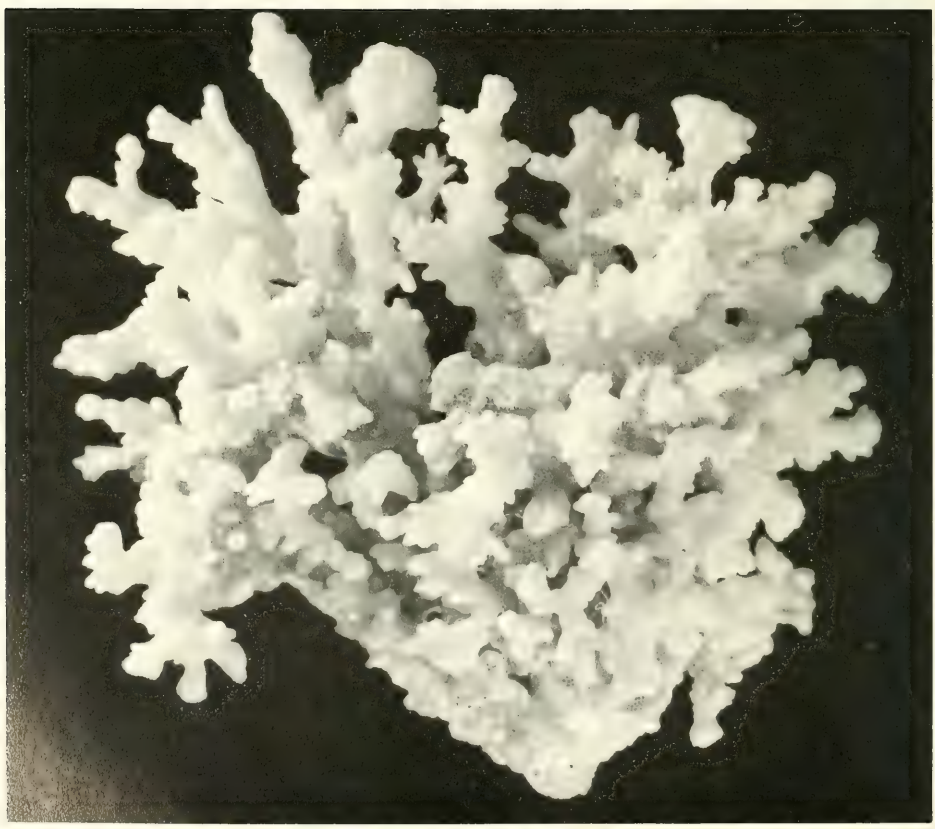

Fig. 2. *Pocillopora* sp. from Cabo San Lucas, Baja California Sur, Mexico. ×0.75.

Fig. 3. Underwater view of *Pocillopora* spp. in turbid waters at Punta Palmillas, Baja California Sur, Mexico.

Fig. 4. Intertidal granite outcropping (middleground) on sandy beach at Punta Palmillas, Baja California Sur, Mexico.

submarine, subparallel, hog-back, granite ridges projecting from the shore into the sea. The coralla are dependent, however, almost entirely upon the granite for support and have not developed a carbonate platform parallel to the shore of classic coral reef structure. Many coralla are exposed at low tides and are a danger to boats. A few very small coralla of *Porites* also are present at Punta Palmillas.

The coral reefs at Bahía Pulmo are similarly supported by several rows of granite ridges which by chance are long and oriented somewhat parallel to the shore, giving the appearance of a concentric series of more classic fringing coral reefs. There also is a richer algal, invertebrate, and vertebrate reef fauna at Bahía Pulmo

Fig. 5. Coralla of *Pocillopora* spp. on intertidal rock shown in Fig. 4.

(Brusca and Thompson 1977) than at the new localities reported here, including large coralla of the hermatypic corals *Pavona* and *Porites* (Squires 1959).

Pocillopora is a hardy coral. At Punta Palmillas, it is abundant on some low rocks (Figs. 4, 5) even though these are intertidal and on an open, coarsely sandy, public beach polluted by great quantities of construction-generated sediment and exposed to storm waves.

I am grateful to Luis Alberto Herrera Gil, Jefe del Departamento de Divulgación Cientifica y Tecnológica, Universidad Autonoma de Baja California Sur at La Paz, for his assistance. J. Wyatt Durham of the Department of Paleontology, University of California, Berkeley, kindly examined a corallum from Punta Palmillas, verified the generic determination, and reviewed an early manuscript. W. K. Emerson of the American Museum of Natural History, New York, graciously supplied some information about the localities of Squires (1959) and reviewed an early version of this note. R. Backe, W. Carney, and S. Goell helpfully assisted with the field work. Voucher specimens collected in December 1987 and February 1988 at Bahía Pulmo, Punta Palmillas, Bahía Chileno, Bahía Santa Maria, and Cabo San Lucas are deposited in the Section of Invertebrate Zoology, Natural History Museum of Los Angeles County. One specimen from Punta Palmillas was retained at the University of California Museum of Paleontology, Berkeley.

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Research Notes

Sizes and Seasonal Abundance of Rock Crabs in Intertidal Channels at James V. Fitzgerald Marine Reserve, California

The rock crab (*Cancer antennarius*) is a common inhabitant of rocky intertidal zones and shallow subtidal areas along the coast of California (Garth and Abbott 1980). There are no data on the seasonal abundance and adult/juvenile ratios of rock crabs in an intertidal area. The present study was undertaken as part of a survey of intertidal animals in a heavily visited part of James V. Fitzgerald Marine Reserve, Moss Beach, San Mateo County.

The rocky intertidal zone of the reserve is bordered by coastal bluffs and coarse sand beaches on the landward side and a surf-swept region at seaward edge. Crabs have been protected by law here since 1969. Sea otters (*Enhydra lutris*), major predators on crabs, rarely stray this far north.

Study sites were established in three areas between San Vicente Creek and Seal Cove: the Rocky Lagoon, the Channel and Surf Grass Flats, and South Moss Beach. The sites were located between the 0.0 and −0.2 m tidal levels. All three sites were low-lying rocky areas protected from strong surf on at least two sides by higher rocky reefs. Each of the three sites had a surge channel that gave the area a direct connection to the ocean. For purposes of this study, we avoided exposed, relatively flat rocky areas, where the crabs rarely live; and deep tide pools, where crabs are difficult to observe.

The sites were divided into six transects of 11–30 quadrats of 5 m^2. The beginning and end of each transect were marked permanently with a lag bolt set into the shale rock. Transect lines ran perpendicular to the beach. A meter tape was stretched from lag bolt A, nearest to the beach, seaward to lag bolt B. Each transect line ended at the limit of the intertidal zone or at exposed bare rock. Quadrats received two numbers: 1–6 per transect, and 1–30 moving seaward.

Crabs were counted monthly at the three sites. A thirty-meter tape was stretched between permanent markers bolted into the reef. Crabs were counted in each 5 m^2 quadrat by placing a 0.25 m^2 counting frame directly over the tape so that the tape bissected the counting frame. The counting frame was moved along the tape so that crabs were counted wherever they occurred along the tape. Observations usually were made during slack or ebb tide. The crabs in the frame were counted, measured, and sexed if possible. Measurements were made in millimeters across the widest part of the carapace. Crabs 60 mm wide or more were considered to be adults.

Data were analyzed by the Mann-Whitney test to determine if there was a significant difference in the numbers of adults/juveniles per month for the area as a whole. Total numbers of rock crabs per site per month were compared by the same test to determine if there was a significant difference in numbers between sites.

From October 1985 to September 1986, 145 crabs were observed. Of these,

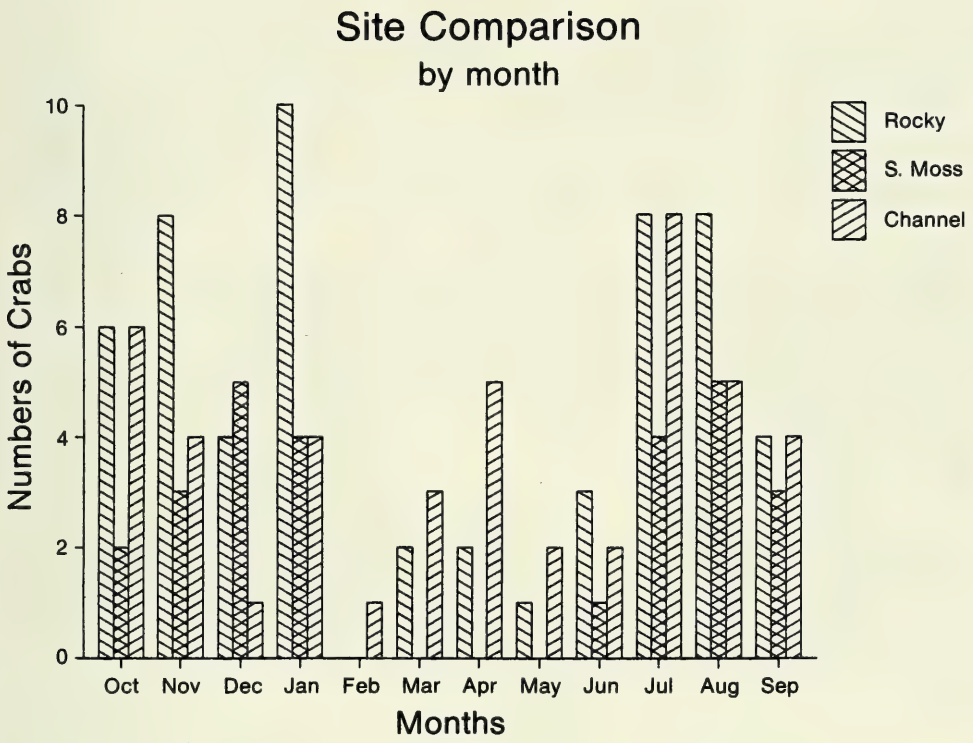

Fig. 1. Total crabs per month at the three sites. Rocky = Rocky Lagoon, S. Moss = South Moss Beach, Channel = Channel and Surf Grass site.

perhaps two sightings in the same quadrat per transect from month to month were of the same individuals. Other crabs differed in size, sex, characteristic color patterns or injuries, so that we were relatively certain that we were not observing the same individual as seen previously. The maximum total number of crabs per month was 23 in July, the minimum was only one in February.

The number of crabs per site varied seasonally. Rocky Lagoon and the Channel and Surf Grass sites tended to have similar numbers of crabs (Fig. 1). South Moss Beach had fewer crabs, probably due to loss of habitat after excessive sand deposits in winter. However, there was no significant difference between the monthly numbers of crabs between sites ($P = .1264$). The lack of crabs in February coincided with intense winter storms, in which waves up to 7 m high were recorded.

Numbers of both adult and juvenile crabs tended to be lower in winter-early spring than during the rest of the year (Fig. 2). Juveniles were most numerous in July. There were no significant differences between the numbers of adults and juveniles counted per month ($P = .3743$). The smallest crab measured was 20 mm and the largest, 125 mm. One or two crabs measuring 30 mm or less were observed per month in October–January, March, July, and September; one to four crabs measuring 31–40 mm were seen in October, November, February, April, June, July, and August. No seasonal trend in settlement of small crabs was evident.

Male *C. antennarius* always outnumbered females, with a yearly average ratio

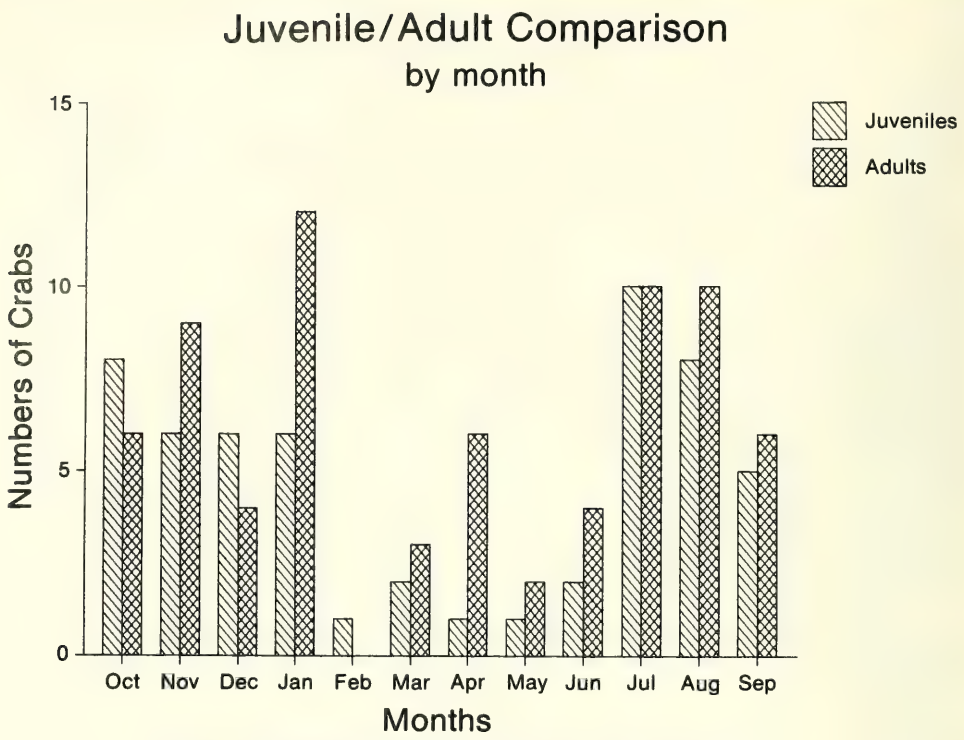

Fig. 2. Juvenile/adult comparison of *C. antennarius* per month.

of 1.6:1. Seasonal male/female ratios did not differ significantly from the yearly average. An ovigerous female (88 mm) was found in November.

Within the transects, the crabs appeared to choose habitat by suitable cover. We found that, with experience, we could predict where the crabs would occur—usually under rocks over 20 cm in largest diameter which either were embedded in sand or gravel or had sufficient space beneath to enable a crab to slip under the rock. These rocks usually had been embedded in the same position for several weeks before the crab moved underneath, and were sufficiently heavy not to be moved except by waves 2 m high or greater. Larger crabs tended to occupy more sheltered spots and juveniles seemed more likely to be found partially buried in sand.

Carroll (1982) studied abundance, sizes and growth of adult *C. antennarius* by a tagging and trapping study at 3–22 m off Diablo Cove, California. In this study of over 9000 crabs, females were more abundant during autumn, but males showed no clear seasonal trends. Only 6.3% of the tagged crabs were recaptured, the majority of them close to their original release site. In a subtidal trapping study, Reilly (1987) found that rock crabs were most abundant in fall. Our results agree generally with those of previous studies: the total number of crabs varied seasonally, with more crabs in summer and fall. The crabs rarely were found in the same spot.

We found that numbers of crabs lessened greatly after severe winter storms. During November–April, there usually are five or more storms with waves of 2–

4 m in height per month. Waves can reach to 7 m high during winter. Much of the habitat previously occupied by crabs at South Moss Beach was buried by sand in winter-spring. The Rocky Lagoon site was inaccessible due to high surf in February. Strong storms overturn rocks and roll them across the flats, crushing intertidal animals. In severe weather, those crabs that cannot find shelter or retreat into deeper areas may be killed—we often found dead, broken crabs cast ashore after storms.

Our results seem to indicate a low population density of rock crabs year-round. In our survey of 1030.50 m^2, the average concentration of crabs was 0.140 crabs per m^2. Carroll (1982) gave a population density depending on season of 1060–10,590 crabs/20 hectares for Diablo Cove. Tegner and Butler (1981) estimated a population density of 0.250 *Cancer* spp. per m^2 off La Jolla, California, at a depth of 10 m. Drummond-Davis et al. (1982) estimated a subtidal population density of one *Cancer irroratus* per 2 m^2.

Acknowledgments

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COVER: *Pocillipora* growing on a granite substrate along the gulf coast of Baja California, Mexico. Photo by Edward C. Wilson. Page 79.